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Storage and release of nutrients during litter decomposition for native and invasive species under different flooding intensities in a Chinese wetland

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ABSTRACT

Projections of climate change impacts over the coming decades suggest that rising sea level will flood coastal wetlands. We studied the impacts of three intensities of flooding on litter decomposition in the native *Cyperus malaccensis*, and the invasives *Spartina alterniflora* and *Phragmites australis* in Shanyutan wetland (Minjiang River estuary, China). Invasive species had larger C, N and P stocks in plant-litter compartments and higher fluxes among plant-litter-soil, which increased with flooding intensity. Litter mass remaining (% of initial mass) were correlated with the N:P ratio in remaining litter, consistently with the N-limitation in this wetland. *P. australis* had the highest accumulated N release ($P < 0.001$) in all flooding intensities, whereas *C. malaccensis* had higher N accumulated release than *S. alternifolia* but only at low flooding intensity. At high flooding intensity, the N released in the first year of litter decomposition ($g\,m^{-2}\,y^{-1}$) were 9.56 ± 0.21, 2.38 ± 0.18 and 1.92 ± 0.03 for *P. australis*, *S. alternifolia* and *C. malaccensis*, respectively. The higher rates of nutrient release from litter decomposition in invasive species provided better nutrient supply during the growing season coinciding with the initial phases of decomposition. Thus, this study shows that invasive species may gain a competitive advantage over the native *C. malaccensis* under the projected scenarios of sea level rises.

1. Introduction

Coastal wetlands occupy $5.7 \times 10^6\,km^2$ globally (3.6% of land surface) (Ramsar, 2013), being important sinks of carbon and nutrients. They are among the ecosystems most affected by global change (Ramsar, 2013). Wetlands are currently affected by global change drivers such as species invasion and land use changes (Wang et al., 2014; Wang et al., 2015a, b,c,d) or/and changes in flooding intensity favored by the rise in sea level or/and change in rivers (flow) (Bueh et al., 2003; Grafton et al., 2013). P is currently accumulating in wetland areas of China (Yan et al., 2016), trend that could be affected by flooding intensity shifts and species invasion. Human driven changes in land-use have reduced the natural wetland areas and therefore their capacity to store C (Hopkinson et al., 2012). This can be detrimental to global C store capacity since coastal wetlands are currently storing $208.4\,C\,g\,m^{-2}\,y^{-1}$, and this capacity could be compromised (Lu, 1999). These systems continue to be lost globally at rates ranging from 1 to 7% annually (Bai et al., 2007; Fraser et al., 2012; Hopkinson et al., 2012; Dominguez-Beisiegel et al., 2013).

Coastal wetlands occupy $1.2 \times 10^4\,km^2$ in China (Shen and Zhu, 1999), and a higher sea level will increase flooding in the current coastal wetlands and create new wetlands farther inland. Most coastal areas in China, however, are protected by seawalls, so wetland areas cannot increase in size and will only decrease as the sea level rises (Yang et al., 2014). Changes in flooding intensity can affect litter mineralization (Tong and Liu, 2009) and thus plant growth (Fan et al., 2015) and community structure (Schrama et al., 2015).

Invasion by plant species in wetland areas has been associated with changes in soil condition, especially elemental composition and nutrient availability (Vourlitis et al., 2011; Wang et al., 2016a,b). Moreover, flooding can affect species distribution and diversity and soil nutrient status (Machado et al., 2015; Wang et al., 2015b, 2016a). Invasive plants are associated with higher soil C and N stocks and N, P and K availabilities (Sardans et al., 2017). This potential impacts of plant invasion can vary and interact with this increase in flooding and also in a context of currently increasing nutrient loads in the wetland

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estuaries in countries as China. We lack information, however, on the effect of the duration of daily flooding on litter decomposition and nutrient dynamics.

Litter is an important pool of C and nutrients in terrestrial ecosystems (Poll et al., 2008; Adair et al., 2008) and is key to recycling in ecosystems by the decomposition of organic matter and release of nutrients (Peng and Liu, 2002). The rate of litter decomposition in wetlands affects the accumulation and retention of C and nutrients (Yin et al., 1994; Wang et al., 2012). Plant invasion and changes in flooding intensity, can thus change litter quantity and quality and therefore affect litter decomposition process (Hättenschwiler and Jørgensen, 2010; Ott et al., 2012) and C and nutrients release rates (Tong and Liu, 2009). This, in turn, would affect soil activity and CO_2 emissions, with the consequent feed-back on global warming and eutrophication process (Hobbie et al., 2002; Zhang et al., 2014).

Invasive trees accelerate litter decomposition rates in riparian flooding wetland forests (Bottollier-Curtet et al., 2011; Mitchell et al., 2011; Buzhdygan et al., 2016). Invasive species have also frequently higher litter production than native species (Ellis et al., 1998; Warren et al., 2001; Sardans et al., 2017) Recent meta-analysis have reported a general trend towards higher soil organic carbon (SOC) and nutrient concentration and availability related to invasive plant success (Sardans et al., 2017). The possible interactive effect of flooding and species invasion on the changes in litter elemental composition and stoichiometry and the rates of nutrient release during litter decomposition has not been studied in coastal wetlands. Therefore the response of the decomposition and nutrient dynamics of the litters of the invasive and native species to the projected increase in flooding (IPCC, 2014) is not known. We should expect a drop in litter decomposition under higher flooding, but several compensatory mechanisms can change this trend. Schmidt et al. (2016) have recently reported higher litter decomposition under flooded-anoxic periods due to the higher activity of litter invertebrates (mesofauna) under flooded anoxic conditions. Furthermore, the higher speed and turbulence of water under higher flooding regimes can contribute to accelerate decomposition by promoting higher physical breaking of litter thus increasing the surface by mass ratio of litter and facilitating the activity of decomposers (Langhans et al., 2008).

We hypothesized that invasive plant species would decompose and release nutrients faster than the native ones, consistent with their higher rates of nutrient cycling via litter decomposition. We secondly hypothesized that this higher and faster nutrient cycling via litter decomposition of invasive versus native plants would probably change under different flooding intensities. Finally, the changes in mass loss and nutrient release during litter decomposition could be also related with initial litter C:N:P stoichiometry and soil properties. Our main goal was to analyze how flooding rise can affect the C, N and P cycling and release capacity from litter in native and invasive species. With this aim, we tested the above mentioned three hypotheses investigating (i) the changes in litter mass and the cycling of C and nutrients of invasive and native plants in estuarine tidal wetlands under different flooding intensities (350, 1050 and 1760 h y^{-1}) and (ii) the relationships of litter nutrient cycling with litter and soil elemental composition.

2. Material and methods

2.1. Study area

This study was conducted in the Shanyutan wetland (26°01′46″N, 119°37′31″E; Fig. 1), the largest tidal wetland (approximately 3120 ha) in the estuary of the Minjiang River. The climate in this region is relatively warm and wet with a mean annual temperature of 19.6 °C and a mean annual precipitation of 1346 mm (Zheng et al., 2006). The soil surface is submerged across the study site beneath 10–120 cm of water for 3–3.5 h during each tidal inundation (Wang et al., 2015b). The soil surface of the entire wetland is exposed at low tide, but the soil remains flooded at some depths, normally water table remains permanent from 20 cm of depth (Wang et al., 2015b). In the lowest tidal periods the minimum water table is about 20 cm below the ground. The average annual weight percentage of water in the soil is 116% [(soil wet weight - soil dry weight)/soil dry weight · 100] and the soil redox is +12.6 mV, respectively (Wang et al., 2015b).

We studied and compared litter decomposition rates among three mono-specific stands: the native plant *C. malaccensis*, the invasive plant *S. alterniflora* (communities > 10 years old) and the invasive plant *P. australis* (communities > 30 years old). These are the three dominant plant species in this estuarine wetland. They are typically found in the upper (mid to high) portions of mudflats. Both *S. alterniflora* and *P. australis* mainly invaded the native *C. malaccensis* wetland, typically found in the upper (mid to high) portions of mudflats. The three species are located in sites with similar flooding intensity, but despite this, wetland soils in areas dominated by *S. alterniflora* and *P. australis* generally have a lower pH and bulk density and a higher salinity than do areas dominated by *C. malaccensis* (Jia et al., 2008). *S. alterniflora* grows between April and December, the highest population height is about 2.3 m, and the shoot density is about 300 m^{-2} (Zhang, 2008). *P. australis* grows between April and October, the highest population height is about 2 m, and the shoot density is about 250 m^{-2} (Zhang, 2008). *C. malaccensis* grows between April and October, the highest population height is about 1.5 m, and the shoot density is about 1000 m^{-2} (Zhang, 2008). The root systems of the three species have similar biomass distributions in the soil profiles, all with substantial biomass below 50 cm of soil surface but with larger biomass fractions in the 0–15 cm soil layer (Tong et al., 2011).

2.2. Experimental design

C. malaccensis, *S. alterniflora* and *P. australis* litter was collected in February 2012. Three replicates of 20 g of each litter were placed in tightly sealed nylon mesh bags, 20 cm long and wide with a mesh size of 0.3 mm, and allowed to decompose (Wang et al., 2016b). The litter was a mixture of foliar and stem litter in the ratios corresponding to annual foliar:stem litter production ratios of each species (Ouyang, 2014). To know the exact proportion of leaf and stem litter in each species, we separated the leaves and the stems litters of each plant to thereafter weigh them. The litterbags were anchored to the substrate and only one side of litterbags contact with the ground. The experiment began in March 2012. Three flooding intensities (low, high and continuous) were tested with the *C. malaccensis*, *S. alterniflora* and *P. australis* litters, decomposing under *C. malaccensis*, *S. alterniflora* and *P. australis* habitats respectively and in three different flooding intensities. The three levels of flooding intensity were 350, 1050 and 1760 h y^{-1} for low, high and continuous flooding intensity, respectively. The distance between pure-species stands of different plant species for the same flooding intensity level was smaller than 20 m. The sampled areas were at a minimum distance of 100–150 m among them (Fig. 1). In the lowest tidal periods the minimum water table is located about 20 cm below the ground. Samples bags were collected 28, 61, 80, 101, 141, 181, 241, 298 and 370 days after the start of the decomposition experiment. In each sampling time the whole bag was removed from each site. We thus had 3 flood conditions × 3 species × 9 time samplings × 3 replicates = 243 samples.

2.3. Sample collection and analysis

The litter from the sample bags was gently washed with water and then oven dried to a constant weight (60 °C for 24–36 h), weighed and then finely ground in a ball mill. We washed the samples with freshwater to remove possible soil particles from the tissues/organs analyzed and at slow flow to avoid leaching of nutrient from inner tissues (Tong and Liu, 2009; Tong et al., 2011). The concentrations of C and N of the litters were determined using a Vario EL III Elemental Analyzer

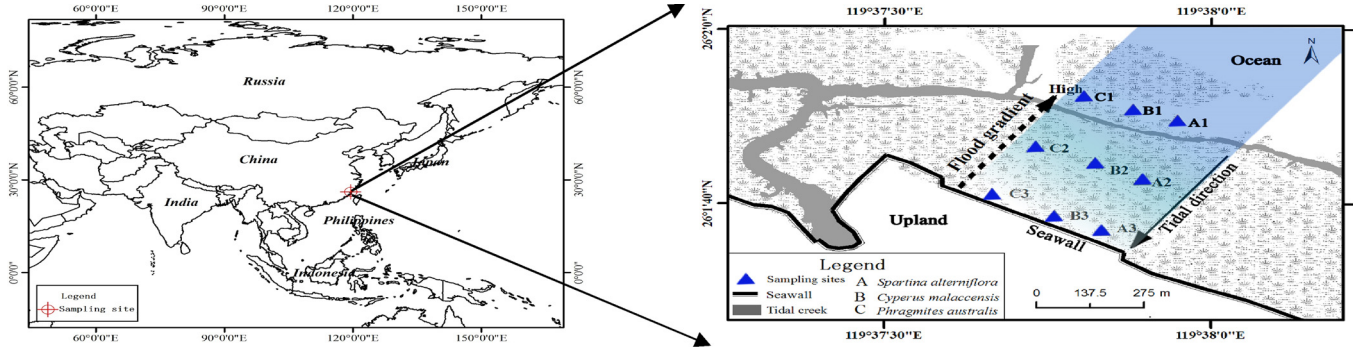

Fig. 1. Location of the sites of litter decomposition for the flood-gradient habitats.

(Elementar Scientific Instruments, Hanau, Germany). P concentration of the litters were measured using the molybdate-blue reaction (Lu, 1999) with a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Kyoto, Japan) after digestion.

2.4. Soil analyses

Soil samples were collected in February 2012 in the Shanyutan wetland from communities dominated by *C. malaccensis*, *S. alterniflora* and *P. australis*. Three plots were randomly established in each community. The samples were collected (0–10 cm) with a small sampler (diameter, 0.1 m). These three samples from each layer were bulked to form one sample per layer. The sampling design consist in: three species communities x three random plots by species x three replicated samples in each plot x 3 flooding level, then 81 samples in total. The soil samples were air-dried and finely ground in a ball mill after the removal of all roots and visible plant remains for the determination of total soil organic carbon (SOC) concentration, total N and P concentrations, salinity and pH.

Total SOC was determined by $K_2Cr_2O_7$-H_2SO_4 digestion and total soil N concentration was determined by total Kjeldahl digestion (Buchi Scientific Instruments, Flawil, Switzerland), and total soil P concentration was determined by perchloric-acid digestion followed by ammonium-molybdate colorimetry and measurement using a UV-2450 spectrophotometer. Soil salinity and pH were measured by a DDS-307 salinity meter (Boqu Scientific Instruments, Shanghai, China) and an 868 pH meter (Orion Scientific Instruments, Waltham, Massashusetts, USA), respectively.

2.5. Response variables

1 Litter mass remaining (% of initial mass) was calculated as the (litter remaining mass / initial litter mass) *100.
2 C, N, P amount remaining in remaining litter (g) was calculated as (the litter remaining mass * C,N,P concentration in remaining litter).
3 C, N, P remaining in remaining litter (% of initial) was calculated as [(the litter remaining mass * C,N,P concentration in remaining litter) / (initial litter mass *C,N,P concentration in initial litter)] *100.
4 Accumulated released of C, N, P (g) from litter was calculated as (initial litter mass (g) * C,N,P concentrations in initial litter) _- (the litter remaining mass (g) * C,N,P concentrations in remaining litter).
5 C:N:P ratios (from mass ratio) in initial and remaining litter were calculated from the corresponding litter C,N,P concentration in initial and in remaining litter.

2.6. Statistical analyses

We analyzed the effects of species (*C. malaccensis*, *S. alterniflora* and *P. australis*), intensity of flooding (low, high and continuous) and time as fixed factors and litter bag replicates as random factor on the studied response variables by using general linear and generalized mixed models. The dependent analyzed variables were elemental concentrations and ratios of the litter, the relative (% from initial) and absolute amounts of C, N and P that still remains in litter, the relative (% from initial) and absolute amounts of C, N and P that have been released from litter, and the C:N, C:P and N:P ratios of the absolute amounts released in each sampling moment during one year of litter decomposition. We used the "nlme" (Pinheiro et al., 2016) and "lme4" (Bates et al., 2015) R packages with the "lm", "lme", "glm" and "glmer" functions. We chose the best model for each dependent variable using R^2-adjusted in the case of lm models and Akaike information criteria in the case of glm and glmer models. We used the MuMIn (Barton, 2012) R package in the mixed models to estimate the percentage of variance explained by the model.

We performed multivariate statistical analyses using general discriminant analysis (GDA) to analyze whether the different litter variables taken altogether discriminate the different species litter decomposition under distinct levels of flooding. We used time as categorical controlling factor. We also determined the variance due to time as an independent categorical variable. The GDAs were performed using Statistica 6.0 (StatSoft, Inc. Tulsa, USA). C:N, C:P and N:P ratios were calculated as mass ratios.

3. Results

Litter mass and C, N and P contents remaining in the litter decreased by about 50% during the first 50 days of decomposition (Figs. 2, 3a,b,c). Flooding intensity generally had a slight effect on the percentage of remaining C, N and P relative to the initial contents during decomposition (Table 1, Figs. 2, 3a–c). Under lower flooding, *C. malaccensis* had the lowest % of the C, N and P contents remaining after the first year of decomposition but this difference with respect the invasive species disappeared at high and continuous flooding intensity. Under continuous flooding intensity, *P. australis* had lowest % of the N contents remaining after the first year of decomposition (Table S1, Fig. 3b).

The C amount remaining in litter and released from litter during the studied year were similar in the three species under high and continuous flooding, whereas at low flooding *P. australis* released more C than the other species (Figs. 4 and 5). *C. malaccesis* released less C, N and P after a year of decomposition at high and continuous flooding than under low flooding. This did not happen in any of both invasive species (Fig. 5). *C. malaccensis* released more N than both invasive species under low flooding intensity whereas *P. australis* released more N under continuous flooding intensity and more P under all flooding intensities than the other two species (Fig. 5). The invasive *P. australis* produced more litter than the other species (Wang et al., 2015c), and this litter also decomposed faster and release more C, N and P during decomposition. These findings were observed in absolute terms at all flooding intensities, due to the higher initial contents of the litter, but

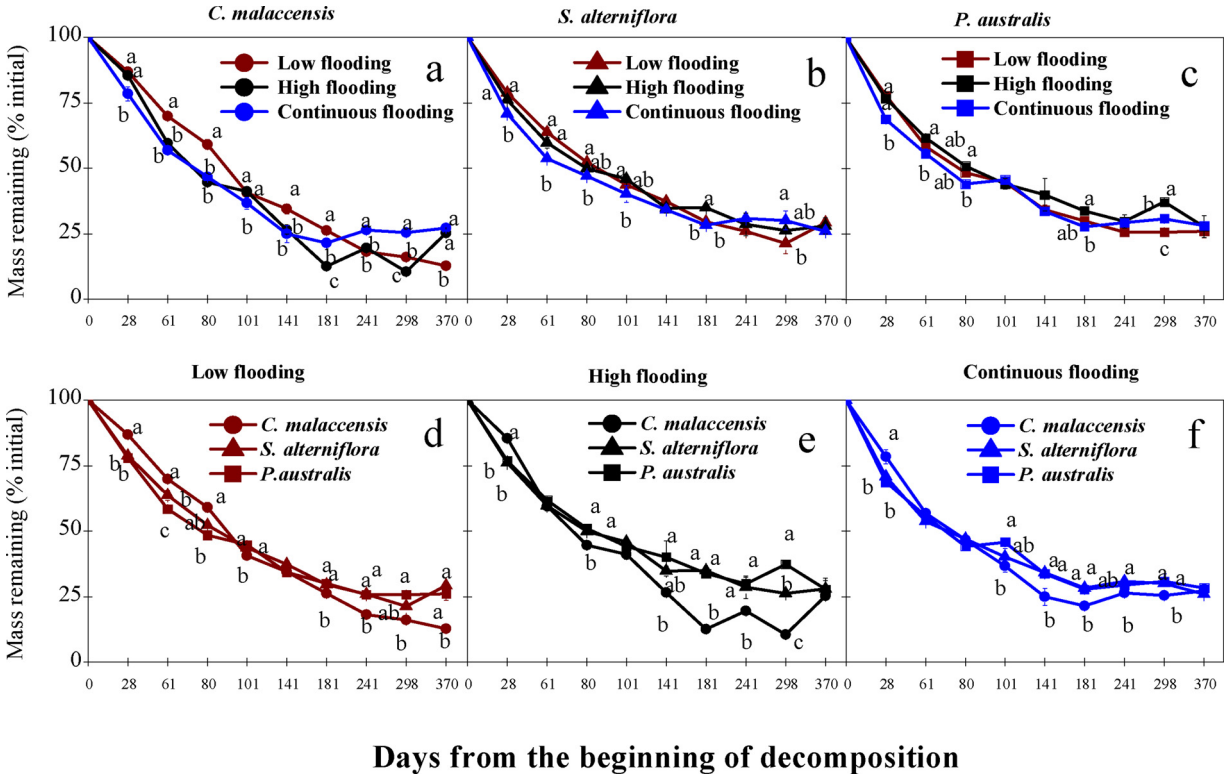

Fig. 2. Mass remaining (%initial, mean ± SE) during the year of litter decomposition in the species, different flooding intensities *for C. malaccensis* (a), *S. alterniflora* (b), *P. australis* (c)) and different plant species for low flooding (d), high flooding (e), continuous flooding (f). Different letters within the graphs indicate statistical differences ($P < 0.05$) between species and flooding intensities.

also in relative terms (lowest % of N initial contents) in continuous-flooding intensity (Table 1, Figs. 2–5). The release of total C, N and P (g released) from the *P. australis* litter was nonetheless less affected by the increases in flooding, followed by *S. alterniflora*, the other invasive species. The litter of the native *C. malaccensis* released more C, N and P under the low- than high- and continuous-flooding intensities (Table 1, Fig. 5). *C. malaccensis* had the lowest litter production and capacity to release C, N and P and was most negatively affected by increases in flooding intensity (Table 1, Figs. 2–5). The unique exception was that *C. malaccensis* released more N (g) during decomposition than *S. alterniflora* under the low-but not under the high- and continuous-flooding intensities (Fig. 5).

Litter C:N concentration ratios tended to decrease slightly for all species and flooding intensities during decomposition (Fig. 6). The litter C:P concentration ratios first increased, then decreased and increased again during the last 100–150 days for several situations but with the degree depending on the species (Fig. 6). The litter N:P concentration increased during the last 130 days in all three species, mainly under the low- and high-flooding intensities (Fig. 6). The litter N:P ratios in the three species were thus lower in the continuous-flooding than in the high- and low-flooding intensities by the end of the year. The mass remaining was correlated positively with litter C:N ($R = 0.54$, $P < 0.0001$) and C:P ($R = 0.33$, $P < 0.0001$) ratios and negatively with litter N:P ratios ($R = -0.28$, $P < 0.0001$) during decomposition (Table S1). Furthermore, the analysis of all the data of the absolute contents of C, N and P released after one year of decomposition indicated a general trend of flooding intensity to decrease the release of C, N and P in *C. malaccensis* (Table S1).

The initial litter C:N ratio was highest in *S. alterniflora*, followed by *P. australis* and *C. malaccensis* (Fig. 6). The initial litter C:P ratio was lowest in *P. australis* and similar between *S. alterniflora* and *C. malaccensis* (Fig. 6). The initial litter N:P ratio was highest in *S. alterniflora*, followed by *P. australis* and *C. malaccensis*. The ratios were higher by the end of the year for all situations, except for the litter from *C. malaccensis* under the low-flooding intensity.

All species under different flooding intensities were separated among them by the GDA model with mass remaining (MR); C:N, C:P and N:P litter concentration ratios; the percentage of initial amounts of C, N and P, the total C, N and P mass in litter remaining and accumulated released form litter, the C:P and N:P ratios of the accumulated release from litter, soil salinity, pH and C, N and P concentrations as the most significant variables in the GDA model (Table 2). Root 1 (explaining the 83.0% of the total variance) was mainly loaded with litter variables and separated different species. The litter N and P concentrations were highest and C concentrations lowest in soils under *C. malaccensis*, whereas the contrary patterns were observed in *S. alternifolia* litter with *P. australis* litter in intermediate position (Fig. 7). Different levels of flooding separated along root 2 (explaining 11.0% of the total variance). Continuous flooded soils had the highest soil P concentrations and the lowest values of C and N concentration and salinity, whereas low flooded soils had the contrary patterns and high flooded soils the intermediate position (Fig. 7).

4. Discussion

4.1. Changes in mass, C and nutrients released during litter decomposition of the three species associated to flooding intensity rises

The impact of flooding intensity on litter elemental composition and the amounts of C, N and P released and remaining during decomposition was species-specific. Flooding had scarce effects on litter accumulated release of C, N and P release in both invasive species but had a negative effect on litter rates of C, N and P release during the 370 first days of decomposition in native species. Under low-flooding intensity *C. malaccensis* had a higher relative (%) from initial release of C, N and P, whereas at high-flooding intensity both invasive species had higher

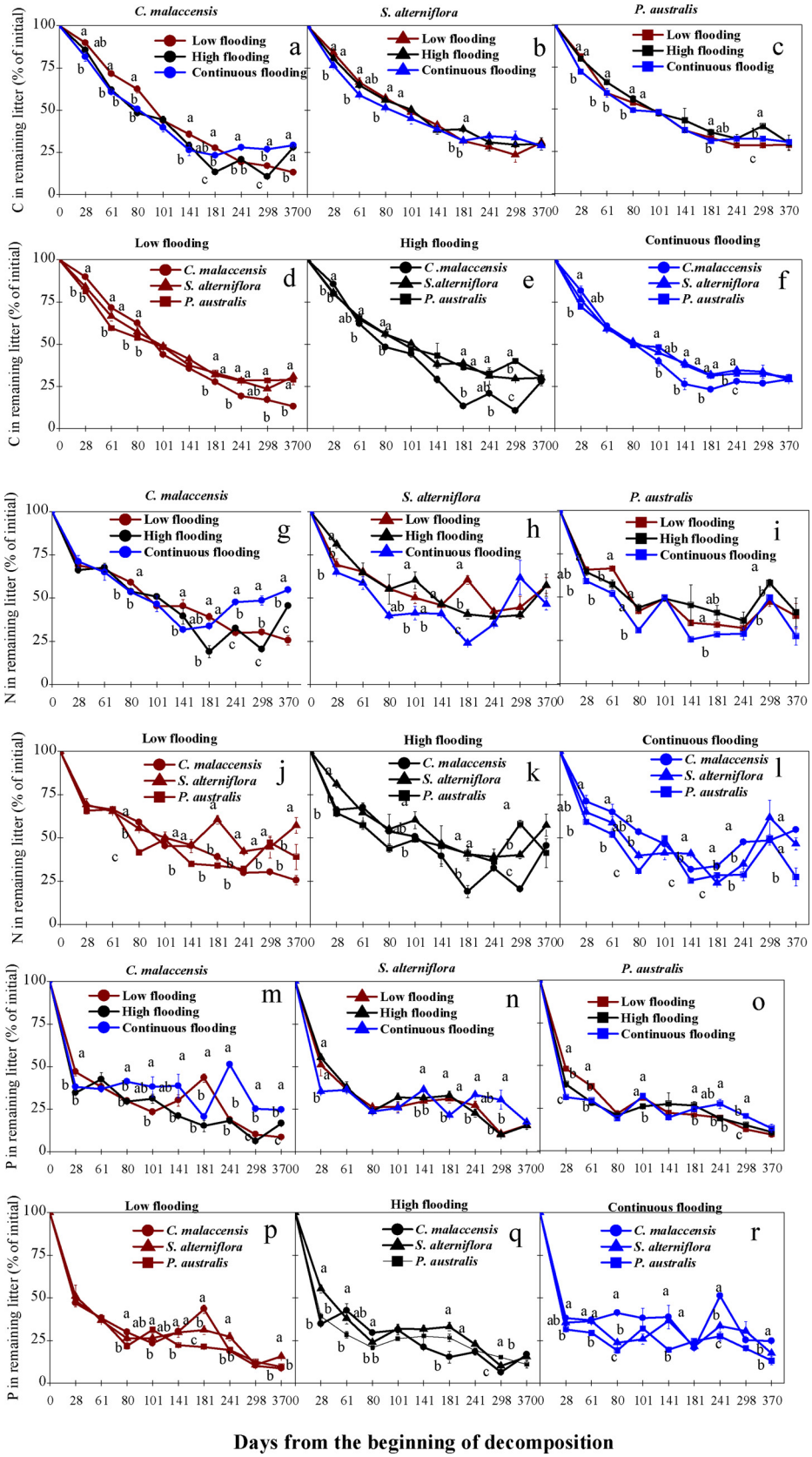

Fig. 3. Amounts of C in remaining litter (%initial, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (a), *S. alterniflora* (b), *P. australis* (c) and different plant species for low flooding (d), high flooding (e), continuous flooding (f). N in remaining litter (% initial, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (g), *S. alterniflora* (h), *P. australis* (i) and different plant species for low flooding (j), high flooding (k), continuous flooding (l). P in remaining litter (%initial, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (m), *S. alterniflora* (n), *P. australis* (o) and different plant species for low flooding (p), high flooding (q), continuous flooding (r). Different letters within the graphs indicate statistical differences ($P < 0.05$) between species and flooding intensities.

relative (%) and absolute (g) release of P and *P. australis* had also higher relative (%) and absolute (g) release of N. Both invasive species released more C, N and P amounts, specially *P. australis*, than the native species, except under low flooding where C. malaccensis released more N than *S. alterniflora*. *S. alternifolia* and mainly *P. australis* released more N and P from their litter during the growing season than the native species. This higher release of C, N and P from litter in invasive species, is in agreement with several previous studies (Sardans et al., 2017) and

Table 1
Linear, mixed and generalized models of the changes in litter elemental composition and released composition during the year of decomposition. The best model was based on the assumption of the normality and homogeneity of remaining distributions using Akaike information criteria. Empty boxes corresponding to interactions mean that this interaction was not significant and had been not included in the corresponding analysis.

Dependent variable	Model	R^2	AIC (Akaike value) of the model	Independent variables							
				Fixed							Random
				Sp	Fl	T	Sp × Fl	Sp × T	Fl × T	Sp × Fl × T	Litter bag replicates
Mass remaining (% initial)	**lm**	**0.66**		**F = 1.54 df = 2 P = 0.22**	**F = 0.32 df = 2 P = 0.72**	**F = 508 df = 1 P < 0.0001**					**No**
Mass remaining (g m^{-2})	**glm**	**0.99**	**3475.5**	**F = 304 df = 2 P < 0.0001**	**F = 0.45 df = 2 P = 0.64**	**F = 845 df = 1 P < 0.0001**		**F = 8.9 df = 14 P = 0.0002**	**F = 6.4 df = 14 P = 0.002**		**No**
[C] in remaining litter	**lm**	**0.27**		**F = 15.6 df = 2 P < 0.0001**	**F = 5.57 df = 2 P = 0.0043**	**F = 59.6 df = 1 P < 0.0001**					**No**
[N] in remaining litter	**lm**	**0.82**		**F = 213 df = 2 P < 0.0001**	**F = 5.4 df = 2 P = 0.005**	**F = 644 df = 1 P < 0.0001**	**F = 5.85 df = 2 P = 0.0002**	**F = 32.6 df = 14 P < 0.0001**	**F = 4.61 df = 14 P = 0.011**		**No**
[P] in remaining litter	**lme**	**0.20**	**-19.62**	**F = 11.6 df = 2 P < 0.0001**	**F = 7.64 df = 2 P < 0.0001**	**F = 0.24 df = 1 P = 0.62**	**F = 6.17 df = 2 P = 0.0024**		**F = 5.08 df = 14 P = 0.0069**		**Yes**
C:N in remaining litter	**lm**	**0.69**		**F = 147 df = 2 P < 0.0001**	**F = 10.8 df = 2 P < 0.0001**	**F = 248 df = 1 P < 0.0001**	**F = 8.73 df = 2 P < 0.0001**				**No**
C:P in remaining litter	**lm**	**0.21**		**F = 10.5 df = 2 P < 0.0001**	**F = 5.33 df = 2 P = 0.0054**	**F = 4.25 df = 1 P = 0.040**	**F = 8.26 df = 2 P = 0.00035**		**F = 6.88 df = 14 P = 0.0012**		**No**
N:P in remaining litter	**lm**	**0.59**		**F = 15.1 df = 2 P < 0.0001**	**F = 24.0 df = 2 P < 0.0001**	**F = 258 df = 1 P < 0.0001**			**F = 23.1 df = 14 P < 0.0001**		**No**
C amount remaining (% initial)	**lm**	**0.70**		**F = 3.13 df = 2 P = 0.038**	**F = 0.177 df = 2 P = 0.84**	**F = 577 df = 1 P < 0.0001**			**F = 3.25 df = 14 P < = 0.040**		**No**
N amount remaining (% initial)	**lme**	**0.39**	**2287.8**	**F = 3.52 df = 2 P = 0.031**	**F = 1.17 df = 2 P = 0.32**	**F = 159 df = 1 P < 0.0001**					**Yes**
P amount remaining (% initial)	**lm**	**0.43**		**F = 1.49 df = 2 P = 0.23**	**F = 0.78 df = 2 P = 0.46**	**F = 198 df = 1 P < 0.0001**					
C amount remaining (g)	**glm**	**0.98**	**3018.6**	**F = 343 df = 2 P < 0.0001**	**F = 0.213 df = 2 P = 0.81**	**F = 874 df = 1 P < 0.0001**	**F = 9.45 df = 2 P = 0.00011**		**F = 7.14 df = 14 P = 0.00096**		
N amount remaining (g)	**lme**	**0.70**	**905.83**	**F = 151 df = 2 P < 0.0001**	**F = 1.7 df = 2 P = 0.19**	**F = 27.8 df = 1 P < 0.0001**		**F = 32.0 df = 14 P < 0.0001**			**Yes**
P amount remaining (g)	**glmer**	**0.73**	**273.63**	**F = 70.8 df = 2 P < 0.0001**	**F = 4.69 df = 2 P = 0.01**	**F = 127 df = 1 P < 0.0001**	**F = 8.3 df = 2 P < 0.0001**				**Yes**
C amount released (g)	**lm**	**0.93**		**F = 792 df = 2 P < 0.0001**	**F = 1.8 df = 2 P = 0.19**	**F = 1167 df = 1 P < 0.0001**	**F = 369 df = 2 P < 0.0001**				**No**
N amount released (g)	**lm**	**0.76**		**F = 286 df = 2 P < 0.0001**	**F = 1.26 df = 2 P = 0.19**	**F = 180 df = 1 P < 0.0001**	**F = 32.0 df = 2 P < 0.0001**				**No**
P amount released (g)	**lm**	**0.79**		**F = 393 df = 2 P < 0.0001**	**F = 0.19 df = 2 P = 0.82**	**F = 177 df = 1 P < 0.0001**	**F = 24.7 df = 2 P < 0.0001**				**No**
C:N released	**lm**	**0.61**		**F = 69.9 df = 2 P < 0.0001**	**F = 0.26 df = 2 P = 0.78**	**F = 246 df = 1 P < 0.0001**	**F = 11.8 df = 2 P < 0.0001**				**No**
C:P released	**lm**	**0.55**		**F = 19.9 df = 2 P < 0.0001**	**F = 2.71 df = 2 P = 0.068**	**F = 281 df = 1 P < 0.0001**					**No**
N:P released	**lm**	**0.37**		**F = 31.5 df = 2 P < 0.0001**	**F = 2.95 df = 2 P = 0.054**	**F = 82.5 df = 1 P < 0.0001**					**No**

SP = Species, Fl = flooding intensity, T = time after beginning of decomposition, F = Fisher statistic.

should confer to both invasive species a competitive advantage in an environment where at least one nutrient, N, is limiting in this wetland area (Wang et al., 2012; Wang et al., 2015b,d) and this advantage increased with flooding intensity. The first half of the studied period of litter decomposition, however, coincided with the growing season, so the higher release of N and P in invasive than native species made even more evident the competitive advantage of invasive species.

All these results are consistent with the previous studies conducted

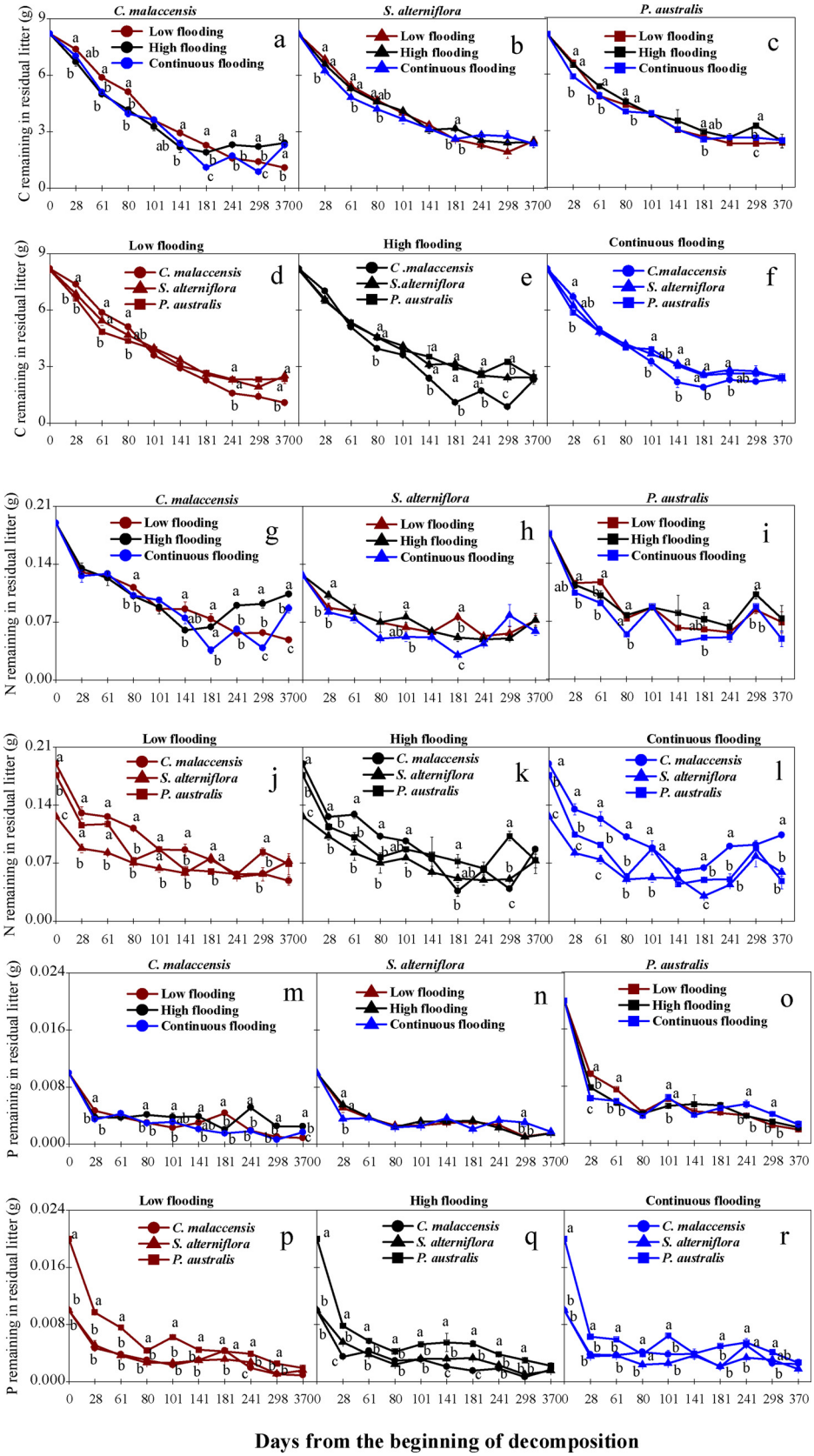

Fig. 4. Amounts of C in remaining litter (g, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (a), *S. alterniflora* (b), *P. australis* (c) and different plant species for low flooding (d), high flooding (e), continuous flooding (f). N in remaining litter (g, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (g), *S. alterniflora* (h), *P. australis* (i) and different plant species for low flooding (j), high flooding (k), continuous flooding (l). P in remaining litter (g, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (m), *S. alterniflora* (n), *P. australis* (o) and different plant species for low flooding (p), high flooding (q), continuous flooding (r). Different letters within the graphs indicate statistical differences ($P < 0.05$) between species and flooding intensities.

in this same wetland area of the estuary of Minjiang River reporting that the biomass was higher in *P. australis* and *S. alterniflora* than *C. malaccensis* (Wang et al., 2015b, 2015c; Tong et al., 2011) and the litter production was highest for the invasive *P. australis* (1450 g $m^{-2} y^{-1}$) followed by *C. malaccensis* (747 g $m^{-2} y^{-1}$) and *S. alternifolia* (653 g $m^{-2} y^{-1}$) (Zhang, 2008; Wang et al., 2015c, d). Our experimental results were also consistent with the observed advantage in biomass production and nutrient and C accumulation in biomass of *P. australis* at

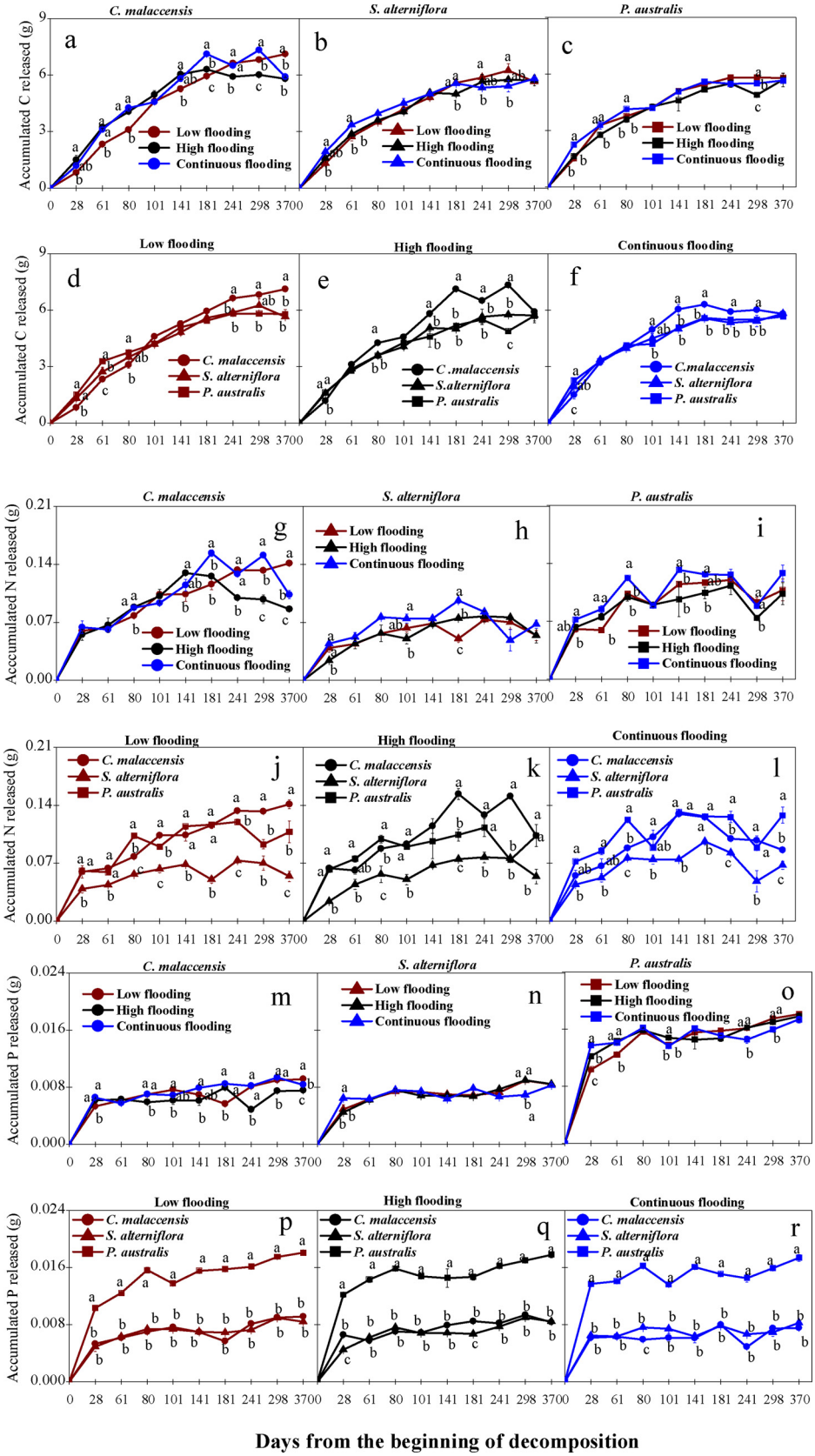

Fig. 5. Accumulated amounts of C released from litter (g, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (a), *S. alterniflora* (b), *P. australis* (c) and different plant species for low flooding (d), high flooding (e), continuous flooding (f). N released from litter (g, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (g), *S. alterniflora* (h), *P. australis* (i) and different plant species for low flooding (j), high flooding (k), continuous flooding (l). P released from litter (g, mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (m), *S. alterniflora* (n), *P. australis* (o) and different plant species for low flooding (p), high flooding (q), continuous flooding (r). Different letters within the graphs indicate statistical differences ($P < 0.05$) between species and flooding intensities.

higher flooding intensities relative to *C. malaccensis* in a previous study in nearby wetland areas of the same river delta (Wang et al., 2015c). Our results also support the faster decomposition of *P. australis* litter in the Yellow River Delta under long-term than intermediate- and short-term flooding reported by Zhao et al. (2015). A previous study comparing growth and nutrient accumulation in plants and soils of *C. malaccensis* and *S. alterniflora* observed consistent results with the current study (Wang et al., 2015d). The results suggest a great capacity of *S.*

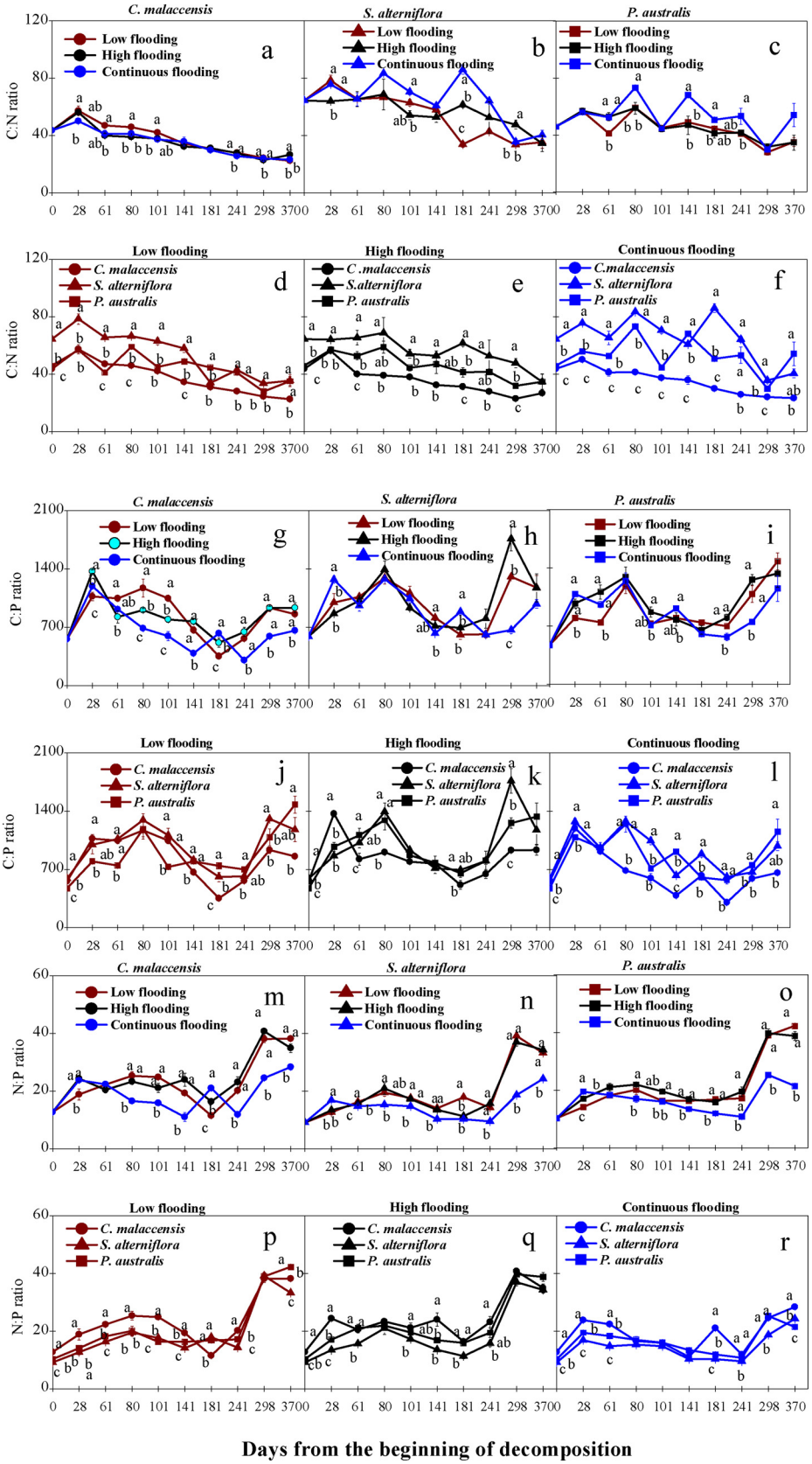

Fig. 6. C:N ratios in remaining litter (mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (a), *S. alterniflora* (b), *P. australis* (c) and different plant species for low flooding (d), high flooding (e), continuous flooding (f). C:P ratios in remaining litter (mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (g), *S. alterniflora* (h), *P. australis* (i) and different plant species for low flooding (j), high flooding (k), continuous flooding (l). N:P ratios in remaining litter (mean ± SE) during the year of litter decomposition, different flooding intensities *for C. malaccensis* (m), *S. alterniflora* (n), *P. australis* (o) and different plant species for low flooding (p), high flooding (q), continuous flooding (r). Different letters within the graphs indicate statistical differences ($P < 0.05$) between species and flooding intensities.

alterniflora to compete with *C. malaccensis* for N, in this N-limited wetland (Wang et al., 2015d).

The higher litter production and absolute higher release of C, N and P but lower release of C, N and P relative to the initial litter amounts for *P. australis* than the native species under the low-flooding intensity has also been observed in other wetlands (Rothman and Bouchard, 2007). *P. australis,* however, is also able to release amounts of C, N and P similar to the initial litter amounts under high and continuous flooding.

Table 2
Statistics (Wilks' λ, F and *P*) of the independent litter variables of the discriminant function analysis among the litters during decomposition. Bold type indicates the statistical significant ($P < 0.05$) of the corresponding variable in the model.

Variable	Wilks' λ	F	*P*
Mass remaining	**0.904**	**2.74**	**0.0068**
C:N ratio	0.935	1.79	0.081
C:P ratio	**0.912**	**2.49**	**0.013**
N:P ratio	0.975	0.66	0.72
C in remaining litter (% of initial)	**0.898**	**2.91**	**0.0042**
N in remaining litter (% of initial)	0.955	1.21	0.29
P in remaining litter (% of initial)	**0.910**	**2.54**	**0.012**
C amount in remaining litter	**0.002**	**1565**	**< 0.0001**
N amount in remaining litter	**0.064**	**374**	**< 0.0001**
P amount in remaining litter	**0.455**	**30.9**	**< 0.0001**
accumulated C released	**0.002**	**16289**	**< 0.0001**
Accumulated N released	**0.057**	**428**	**< 0.0001**
Accumulated P released	**0.412**	**36.8**	**< 0.0001**
C:N of accumulated released	0.957	1.16	0.32
C:P of accumulated released	**0.929**	**1.98**	**0.049**
N:P of accumulated released	0.981	0.511	0.85
Soil C concentration	**0.070**	**340**	**< 0.0001**
Soil N concentration	**0.763**	**8.00**	**< 0.0001**
soil P concentration	**0.074**	**324**	**< 0.0001**
Soil pH	**0.166**	**130**	**< 0.0001**
Salinity (mS cm-1)	**0.551**	**21.0**	**< 0.0001**
Time	0.733	1.03	0.41

Successful invasive species frequently have higher capacities to release N and P due to their faster N and P cycles (Chen et al., 2007; Eppinga et al., 2011) or to higher N and P stocks and fluxes (Windham and Ehrenfeld, 2003; Rothman and Bouchard, 2007) than native species, even though the higher stocks and fluxes of the invasive species have been associated with lower rates of litter decomposition (Liao et al., 2007) than the native species.

In wetland areas with limited water movement, for example with no tidal dynamics or little tidal importance such as in Mediterranean wetlands, an increase in flooding can decrease decomposition, because the higher water availability can initially increase microbial activity and thereby decrease oxygen content and thus slow decomposition (Menéndez and Sanmartí, 2007). However, in the studied subtropical coastal wetland, the rapid turnover of water with large daily movements by strong tides should prevent anoxic conditions. Water turnover is positively correlated with the rates of N and P release from litter (Lee and Kim, 2014). High fungal activity during the decomposition of *P. australis litter,* even in submerged conditions (Kominkova et al., 2000), may account for the lack of a negative effect of flooding on the rates of decomposition in this species. For some wetland species, flooding can frequently increase the rates of the initial leaching phase of decomposition and the acceleration of overall litter decomposition (Neckles and Neill, 1994; Sun et al., 2012). Our results are consistent with those of most previous studies showing that flooding has an important role, but less than species, in the rates of C, N and P release during decomposition and that this role is species-specific, being the slowing nutrient release from litter higher in native than in invasive species with flooding.

4.2. Wetland C and nutrient cycles

Our results thus suggest that this wetland area would continue to retain nutrients (also with higher biomass and litter production) if *C. malaccensis* were replaced by the invasive species, and mainly by *P. australis.* The large capacity and importance of wetland areas to filter nutrients between river and ocean water (Kao et al., 2003) has become an important issue, especially in a region such as southern China where rivers transport large amounts of N and P from human activities such as intensive agriculture. We observed that the studied soil variables such as total soil P and N concentrations did not change under different species but only under different level of flooding. Thus, in spite of litter accumulated more C, N and P after one year of decomposition under both invasive species in all flooding intensity conditions, at this moment after 10–30 years of invasion success total soil P and N concentrations have not changed significantly. The results suggest that, in the projected scenarios of rises in sea level in which most of the remaining coastal wetlands of the main China estuaries come under progressively higher flooding intensities, invasive species such as *S. alterniflora* and *P. australis* can gain an even more competitive advantage over the native *C. malaccensis* by its better nutrient supply from the decomposition of their litter.

4.3. Wetland stoichiometry and litter decomposition

The fresh litter N:P ratio in our study, 10–15, clearly suggested N-limitation. Güsewell and Verhoeven (2006) reported an initial litter N:P threshold on a mass basis of ~25 between N- and P-limited decomposability for grasses. In fact the litter N:P increased for all species and flooding intensities during decomposition, with N concentrations tending to continuously increase and P concentrations to remain more or less constant, suggesting that the microbial decomposers retained proportionally more N than P. The analysis of all data (including all species and flooding intensities) indicated that the litter concentrations of N and P were negatively correlated with the mass remaining in the litter. This relationship, however, was stronger for N than P, and the mass remaining was negatively correlated with the litter N:P ratio. Litter proportionally richer in N than P thus decomposed faster, consistent with the limiting role of N in decomposition previously reported for this area. The accumulation of a nutrient in litter during its decomposition is a good proxy for detecting its limiting role in this biological process (Davis et al., 2003: Güsewell and Verhoeven, 2006). Our results are thus consistent with the importance attributed to the C:N:P ratios of litter for the rates of N and P release during litter decomposition in wetlands (Güsewell and Freeman, 2005; Manzoni et al., 2010; Sun et al., 2012). Results are consistent with the higher soil P concentrations observed under continuous flooding because the N:P ratio of litter remaining increase less than under low and intermediate levels of flooding. Then the higher P retention in litter under continuous flooding was associated with higher soil P concentrations. Moreover, both invasive species had higher C, N and mainly P remaining in litter than the native species. All these results suggest a trend towards higher P accumulation in soils of wetlands with increasing flooding and invasive species occupation.

5. Conclusions and final remarks

Changes in species composition due to flooding and the arrival of invasive species can thus change the N:P ratio of the plant soil-system throughout decomposition, which may contribute to the global changes in N:P ratios observed in several ecosystems mainly due directly or indirectly to human activities (Sardans et al., 2012; Sardans and Peñuelas, 2014; Peñuelas et al., 2012, 2013) specially in water ecosystems of intense industrial and cropland areas of economical emerging countries (Yan et al., 2016).The results suggest that invasive species such as *S. alterniflora* and *P. australis*, which are already widely distributed, can gain a greater competitive advantage over the native *C. malaccensis* by their better nutrient supply from the decomposition of their litter in high flooding conditions. This should be more probable in the projected scenarios of rises in sea level in which most of the remaining coastal wetlands of the main China estuaries come under progressively higher flooding intensities. This advantage would also be augmented by the higher rates of N and P release in the initial phases of litter decomposition during the growing season, the season with higher demands for N and P. The results highlight the importance of the interactions among the different global change drivers, here species

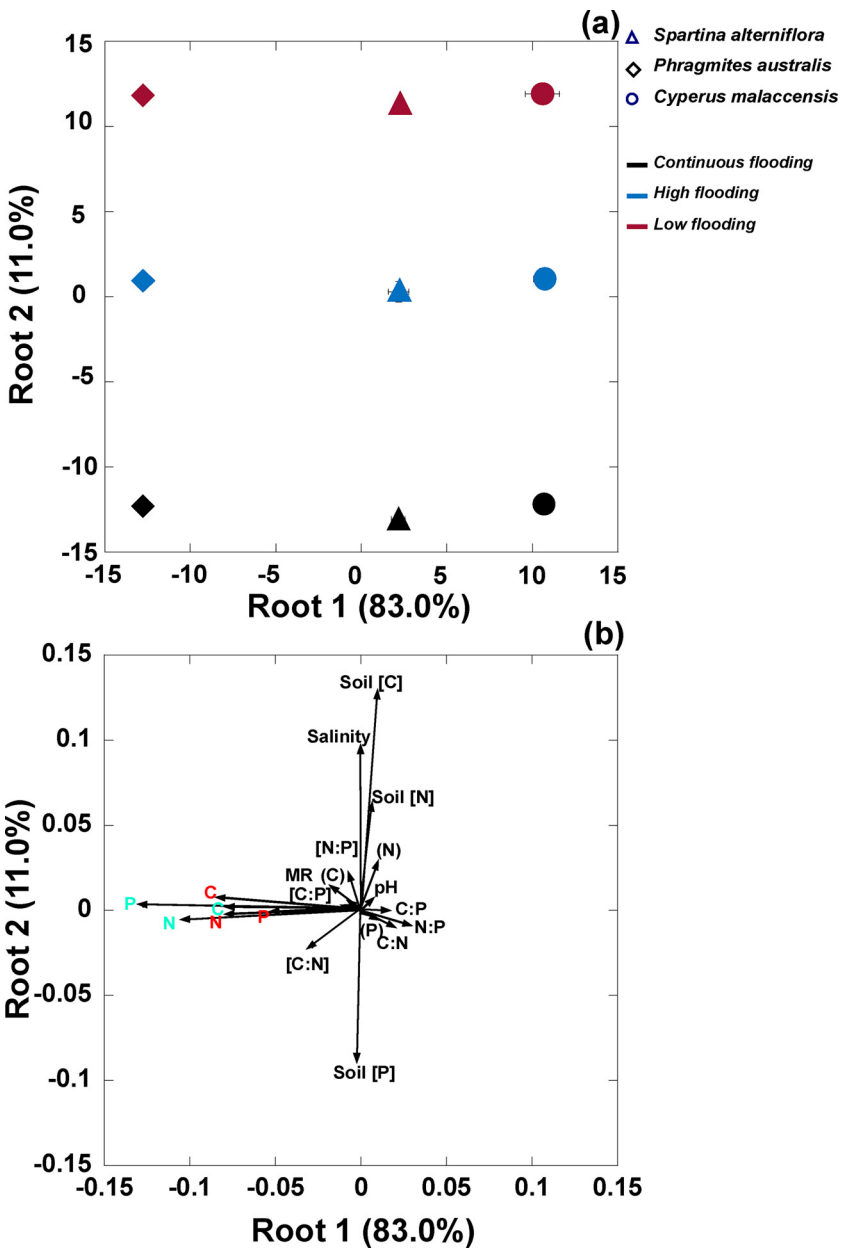

Fig. 7. Discriminant general analysis (DGA) of mass remaining (MR); C:N ([C:N]), C:P ([C:P]) and N:P ([N:P]) litter concentration ratios; the percentage of initial amounts of C (C), N (N) and P (P), the C, N and P of accumulated released from (in green) and remaining in (red) litter, C:N, C:P and N:P ratios of the accumulated release from litter, soil salinity, pH and C (Soil [C]), N (Soil [N]) and P (Soil [P]) concentration during litter decomposition for the various flooding intensities and species as grouping factors. We also considered the portion of the variance due to time as an independent categorical variable (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

invasion and rise in sea level that according to our results should act accelerating the invasive success against native species. In this case invasive species with higher size and capacity to store N and probably other nutrients take advantage of the increases in flooding intensity. This should provide a higher wetland capacity to act as N and P and probably C sinks, thus preventing eutrophication of coastal areas and helping to mitigate atmospheric CO_2 rising, but also should accelerate the wetland silting and disappearance of native species in wide areas.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aquabot.2018.04.006.

References

Adair, E.C., Parton, W.J., Del Grosso, S.J., Silver, W.L., Harmon, M.E., Hall, S.A., Burke, I.C., Hart, S.C., 2008. Simple three-pool model accurately describes patterns of long term litter decomposition in diverse climates. Global Change Biol. 14, 2636–2660.
Bai, J., Cui, B., Deng, W., Yang, Z., Wang, Q., Ding, Q., 2007. Soil organic carbon contents of two natural inland saline-alkalined wetlands in northeastern China. J. Soil Water Conserv. 62, 447–452.
Barton, K., 2012. MuM. In: Multi-model Inference. R Package Version 1.7.2. Http://CRAN. R-283 Project.org/Package=MuMIn. at Http://cran.r-Project.org/Package=MuMIn.
Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.
Bottollier-Curtet, M., Charcosset, J.Y., Planty-Tabacchi, A.M., Tabacchi, E., 2011. Degradation of native and exotic riparian plant leaf litter in a floodplain pond. Freshw. Biol. 56, 1798–1810.
Bueh, C., Cubasch, U., Hagemann, S., 2003. Impacts of global warming on changes in the East Asian monsoon and the related river discharge in a global time-scale experiment. Clim. Res. 24, 47–57.

Buzhdygan, O.Y., Rudenko, S.S., Kazanci, C., Patten, B.C., 2016. Effect of invasive black locust (*robinia pseudoacacia* L.) On nitrogen cycle in floodplain ecosystem. Ecol. Model. 319, 170–177.
Chen, H.L., Li, B., Fang, C.M., Chen, J.K., Wu, J.H., 2007. Exotic plant influencces soil nematode communities through litter input. Soil. Biol. Biochem. 39, 1782–1793.
Davis, S.E., Corronado-Molina, C., Childers, D.L., Day, J.W., 2003. Temporally dependent C, N, and P dynamics associated with the decay of Rizophora mangle L. leaf litter in oligotrophic mangrove wetlands of the Southern Everglades. Aquat. Bot. 75, 199–215.
Dominguez-Beisiegel, M., Herrero, J., Castaneda, C., 2013. Saline wetland' fate in inland deserts: an example of 80 years' decline in Monegros. Spain. Land Degrad. Dev. 24, 250–265.
Ellis, L.M., Crawford, C.S., Molles, M.C., 1998. Comparison of litter dynamics in native and exotic riparian vegetation along the middle Rio Grande of central New Mexico. USA. J. Arid Environ. 38, 283–296.
Eppinga, M.B., Kaproth, M.A., Collins, A.R., Molofsky, J., 2011. Litter feedbacks, evolutionary change and exotic plant invasion. J. Ecol. 99, 503–514.
Fan, P., Zhang, S., Chu, D., Shi, X., 2015. Decomposition of *Suaeda salsa* and *Phragmites australis* in the degraded wetland of Shaohai: species and tissue difference implications on ecosystem restoration. J. Soil Water Conserv. 70, 322–328.
Fraser, M.A., Baldwin, D.S., Rees, G.N., Silvester, E.J., Whitworth, K.L., 2012. Rehabilitation options for inland waterways impacted by sulfidic sediments - Field trials in a south-eastern Australian wetland. J. Environ. Manage. 102, 71–78.
Grafton, R.Q., Pittock, J., Davis, R., Williams, J., Fu, G.B., Warburton, M., Udall, B., McKenzie, R., Yu, X.B., Che, N., Connell, D., Jiang, Q., Kompas, T., Lynch, A., Norris, R., Possingham, H., Quiggin, J., 2013. Global insights into water resources, climate ghange and governance. Nat. Clim. Change 4, 315–321.
Güsewell, S., Freeman, C., 2005. Nutrient limitation and enzyme activities during litter decomposition of nine wetland species in relation to litter N:P ratios. Funct. Ecol. 19, 582–593.
Güsewell, S., Verhoeven, J.T.A., 2006. Litter N:P ratios indicate whether N or P limits the decomposability of graminoid leaf litter. Plant Soil 287, 131–143.
Hättenschwiler, S., Jørgensen, H.B., 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. J. Ecol. 98, 754–763.
Hobbie, S.E., Nadelhoffer, K.J., Hogberg, P., 2002. A synthesis: the role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant Soil 242, 163–170.
Hopkinson, C.S., Cai, W.J., Hu, X., 2012. Carbon sequestration in wetland dominated coastal systems - a global sink of rapidly diminishing magnitude. Curr. Opin. Env. Sust. 4, 186–194.
IPCC, 2014. Regional chapters: Asia. Climate change 2014: impacts, adaptation, and vulnerability. Working group. II. Int. Panel Climate Change.
Jia, R.X., Tong, C., Wang, W.Q., Zeng, C.S., 2008. Organic carbon concentrations and storages in the salt marsh sediments in the Min River estuary. Wetl. Sci. 6, 492–499.
Kao, J.T., Titus, J.E., Zhu, W.X., 2003. Differential nitrogen and phosphorus retention by five wetland plant species. Wetlands 23, 979–987.
Kominkova, D., Kuehn, K.A., Busing, N., Steiner, D., Gessner, M.O., 2000. Microbial biomass, growth, and respiration associated with submerged litter of *Phragmites australis* decomposing in a litoral reed stand of a large lake. Aquat. Microb. Ecol. 22, 271–282.
Langhans, S.D., Tiegs, S.D., Gessner, M.O., Tockner, K., 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. Aquat. Sci. 70, 337–346.
Lee, B.E., Kim, J.G., 2014. The effect of water turnover time decomposition of wild rice (*Zizania latifolia*) and nutrient dynamics in an artificial wetland system. J. Ecol. Environ. 37, 13–19.
Liao, C.Z., Luo, Y.Q., Jiang, L.F., Zhou, X.H., Wu, X.W., Fang, C.M., Chen, J.K., Li, B., 2007. Invasion of *Spartina alterniflora* enhance ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China. Ecosystems 10, 1351–1361.
Lu, R.K., 1999. Analysis Methods of Soil Science and Agricultural Chemistry. Agriculture Science and Technology Press, Beijing.
Machado, N.G., Sanches, L., Silva, L.B., Novais, J.W.Z., Aquino, A.M., Biudes, M.S., Pinto, O.B., Nogueira, J.S., 2015. Soil nutrients and vegetation structure in a neotropical seasonal wetland. Appl. Ecol. Env. Res. 13, 289–305.
Manzoni, S., Trofymow, J.A., Jackson, R.B., Porporato, A., 2010. Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. Ecol. Monog. 80, 89–106.
Menéndez, Margarita, Sanmartí, Neus, 2007. Geratology and decomposition of Spartina versicolor in a brackish Mediterranean marsh. Estuarine Coastal Shelf Sci. 74, 320–330.
Mitchell, J.D., Lockaby, B.G., Brantley, E.F., 2011. Influence of Chinese Privet (*Ligustrum sinense*) on decomposition and nutrient availability in riparian forests. Invas. Plant Sci. Mana. 4, 437–447.
Neckles, H.A., Neill, C., 1994. Hydrologic control of litter decomposition in seasonally flooded praire marshes. Hydrobiologia 286, 155–165.
Ott, D., Rall, B.C., Brose, U., 2012. Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry. Philos. T. R. Soc. B. 367, 3025–3032.
Ouyang, L.M., 2014. Litter Decomposition and Nutrient Dynamics in the Minjiang River Estuarine Wetland, Master Thesis. Fujian Normal University.
Peng, S.L., Liu, Q., 2002. The dynamics of forest litter and its responses to global warming. Acta Ecol. Sin. 22, 1534–1544.
Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., Van der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusià, J., Nardin, E., Vicca, S., Obersteiner, M., Janssens, I.A., 2013. Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. Nat. Commun. 4, 2934.
Peñuelas, J., Sardans, J., Rivas-Ubach, A., Janssens, I.A., 2012. The human-induced imbalance between C, N and P in earth's life system. Global Change Biol. 189, 5–8.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Core, T.R., 2016. Nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3. pp. 1–126. http://CRAN.
Poll, C., Marhan, S., Ingwersen, J., Kandeler, E., 2008. Dynamics of litter carbon turnover and microbial abundance in a rye detritusphere. Soil Biol. Biochem. 40, 1306–1321.
Ramsar, 2013. The Ramsar Manual, 6th edition. Ramsar Convention Secretariat, Switzerland, pp. 110.
Rothman, E., Bouchard, V., 2007. Regulation of carbon processes by macrophyte species in a Garraf lakes coastal wetland. Wetlands 27, 1134–1143.
Sardans, J., Bartrons, M., Margalef, O., Gargallo-Garriga, A., Janssens, I.A., Ciais, P., Obersteiner, M., Sigurdsson, B.D., Chen, H.Y., Peñuelas, J., 2017. Plant invasion is associated with higher plant-soil nutrient concentrations in nutrient-poor environments. Glob.Change Biol. 23, 1282–1291.
Sardans, J., Peñuelas, J., 2014. Hydraulic redistribution by plants and nutrient stoichiometry: shifts under global change. Ecohydrology 7, 1–20.
Sardans, J., Rivas-Ubach, A., Peñuelas, J., 2012. The C: N: P stoichiometry of organisms and ecosystems in A changing world: a review and perspectives. Perspect. Plant Ecol. 14, 33–47.
Schmidt, A., John, K., Auge, H., Brandl, R., Horgan, F.G., Settele, J., Zaisev, A.S., Wolters, V., Schadler, M., 2016. Compensatory mechanisms of litter decomposition under alternating moisture regimes in tropical rice fields. Appl. Soil Ecol. 107, 79–90.
Schrama, M., van Boheemen, L.A., Olff, H., Berg, M.P., 2015. How the litter-feeding bioturbator *Orchestia gammarellus* promotes late-successional saltmarsh vegetation. J. Ecol. 103, 915–924.
Shen, H.T., Zhu, J.R., 1999. The land and ocean interaction in the coastal zone of China. Mar. Sci. Bull. 18, 11–17.
Sun, Z., Mou, X.J., Liu, J.S., 2012. Effects of flooding regimes on the decomposition and nutrient dynamics of *Calamagrostis angustifolia* litter in the Sanjiang plain of China. Environ. Earth Sci. 66, 2235–2246.
Tong, C., Liu, B.G., 2009. Litter decomposition and nutrient dynamics in different tidal water submergence environments of estuarine tidal wetland. Geogr. Res. 28, 118–128.
Tong, C., Zhang, L., Wang, W., Gauci, V., Marrs, R., Liu, B., Jia, R., Zeng, C., 2011. Contrasting nutrient stocks and litter decomposition in stands of native and invasive species in a sub-tropical estuarine marsh. Environ. Res. 111, 909–916.
Vourlitis, G.L., Lobo, F.D., Biudes, M.S., Ortiz, C.E.R., Nogueira, J.D., 2011. Spatial variations in soil chemistry and organic matter content across a *Vochysia divergens* invasion front in the Brazilian Pantanal. Soil Sci. Soc. Am. J. 75, 1554–1561.
Wang, W., Sardans, J., Zeng, C., Tong, C., Wang, C., Peñuelas, J., 2016a. Impact of plant invasion and increasing floods on total soil phosphorus and its fractions in the Minjiang River estuarine wetlands. China. Wetlands 36, 21–36.
Wang, W., Sardans, J., Tong, C., Wang, C., Ouyang, L., Bartrons, M., Peñuelas, J., 2016b. Typhoon enhancement of N and P release from litter and changes in the litter N:P ratio in a subtropical tidal wetland. Environ. Res. Lett. 11, 014003.
Wang, W., Wang, C., Sardans, J., Min, Q., Zeng, C., Tong, C., Peñuelas, J., 2015a. Agricultural land use decouples soil nutrient cycles in a subtropical riparian wetland in China. Catena 133, 171–178.
Wang, W., Wang, C., Sardans, J., Tong, C., Jia, R.X., Zeng, C., Peñuelas, J., 2015b. Flood regime affects soil stoichiometry and the distribution of the invasive plants in subtropical estuarine wetlands in China. Catena 128, 144–154.
Wang, W., Sardans, J., Wang, C., Zeng, C., Tong, C., Asensio, D., Peñuelas, J., 2015c. Ecological stoichiometry of C, N, and P of invasive Phragmites australis and native Cyperus malaccensis species in the Minjiang River tidal estuarine wetlands of China. Plant Ecol. 216, 809–822.
Wang, W., Wang, C., Sardans, J., Zeng, C., Tong, C., Peñuelas, J., 2015d. Plant invasive success associated with higher N-use efficiency and stoichiometric shifts in the soil–plant system in the Minjiang River tidal estuarine wetlands of China. Wetl. Ecol. Manag. 23, 865–880.
Wang, W., Sardans, J., Zeng, C., Zhong, C., Li, Y., Peñuelas, J., 2014. Response of soil nutrient concentrations and stoichiometry to increased human disturbance in a subtropical tidal wetland. Geoderma 232-234, 459–470.
Wang, W., Wang, C., Liu, B., 2012. Effect of salinity on carbon, nitrogen and phosphorus stoichiometry during the decomposition of wetland litter. China Environ. Sci. 32, 1683–1687.
Warren*, R. Scott, Fell, Paul E., Jonna Grimsby, Jonna L., Buck, Erika L., Chris Rilling, G., Fertik, Rachel A., 2001. Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within tidelands of the lower connecticut river. Estuaries 24, 90–107.
Windham, L., Ehrenfeld, J.G., 2003. Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. Ecol. Appl. 13, 883–896.
Yan, Z., Han, W., Peñuelas, J., Sardans, J., Elser, J.J., Du, E., Reich, P.B., Fang, J., 2016. Phosphorus accumulates faster than nitrogen globally in freshwater ecosystems under anthropogenic impacts. Ecol. Lett. 19, 1237–1246.
Yang, Y., Peng, M., Liu, M., Zhao, A., 2014. Effect of sea level rising on the coastal areas of China. Energ. Environ. 32, 237–246.
Yin, C.J., Hang, D.H., Chen, Z.Z., 1994. Quantitative relationships between the litter decomposition of four species in innerMongolia grassland and climatic factors. Acta Ecol. Sin. 14, 149–154.
Zhang, L., Wang, H., Zou, J.W., Rogers, W.E., Siemann, E., 2014. Non-native plant litter enhances soil carbon dioxide emissions in an invaded annual grassland. Plos One 9, e92301.
Zhang, L.H., 2008. Net Primary Productivity and Nitrogen and Phosphrous Dynamics of Dominant Plants in the Wetland of Minjiang River Estuary. Fujian Normal University.
Zhao, Q.Q., Bai, J.H., Liu, P.P., Gao, H.F., Wang, J.J., 2015. Decomposition and carbon and nitrogen dynamics of *Phragmites australis* litter as affected by flooding periods in coastal wetlands. Clean Soil Air Water 43, 441–445.
Zheng, C.H., Zeng, C.S., Chen, Z.Q., Lin, M.C., 2006. A study on the changes of landscape pattern of estuary wetlands of the Minjiang River. Wetl. Sci. 4, 29–34.